AN ABSTRACT OF THE THESIS OF Frank A. Camacho for the Master of Science in Biology presented August 7, 1997.

Title: Size-specific predation by the prawn *Macrobrachium lar* on the freshwater snail *Thiara granifera*.

Approved: ____
Stephen G. Nelson, Chairperson, Thesis Committee

The feeding behavior of the freshwater prawn *Macrobrachium lar* preying on the freshwater gastropod *Thiara granifera* was observed in the laboratory. To expose the prey, the prawn peels the shell of *T. granifera* with its mandibles rather than crushing the shell with its chelae. Peeling was usually initiated along the lip of the aperture except among the smallest prey, in which case *M. lar* would occasionally eat away at the shell from the tip of the spire until reaching the body whorl.

In laboratory feeding assays, *Macrobrachium lar* attacked and preyed more successfully on small snails than large snails. Shell lip strength of *Thiara granifera* was positively correlated with snail size, measured as aperture width, whereas release time of *M. lar* preying on *T. granifera* was inversely related. In these trials, the majority of both size classes of snails was attacked, but the majority of the successful attacks was on the smaller snails.

Smaller specimens of *Thiara granifera* were most susceptible to predation by both sizes of prawns because of the effects of increased mechanical resistance and decreased predator interest (i.e., release time) in large prey as snail size increased.

Both large and small prawns consumed greater amounts of small, versus large, prey because the shells of small *T. granifera* were easier to break.

TO THE OFFICE OF GRADUATE SCHOOL AND RESEARCH

The members of the Committee approve the thesis of Frank A. Camacho presented August 7, 1997.

Stephen G. Nelson, Chairperson

Charles E. Birkeland, Member

H. Galt Siegrist, Member

Barry D. Smith, Member

ACCEPTED:

JOYCE MARIE CAMACHO
Acting Dean, Graduate School and Research

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DATE

Size-specific predation by the prawn *Macrobrachium lar* on the freshwater snail *Thiara granifera*

by

FRANK A. CAMACHO

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INTRODUCTION

Predation on shelled gastropods by decapod crustaceans has been extensively studied in the marine environment, with most predators peeling or crushing their prey (e.g., Bertness and Cunningham, 1981; Geller, 1982; Vermeij, 1982). Similarly, vertebrate predators have been shown to effectively control population densities and distributions of freshwater gastropods (Vermeij and Covich, 1978; Brown and DeVries, 1985; Brönmark, 1988). In contrast, few studies have explored crustacean predation on freshwater snails. Roberts and Kuris (1990) demonstrated that control of laboratory populations of the pulmonate snail *Biomphalaria glabrata*, an intermediate host of human schistosomiasis, could be controlled by a predator, the giant Malaysian prawn *Macrobrachium rosenbergii*. Similarly, the freshwater crab *Somaniathelphusa sinensis* preys upon members of the prosobranch family Thiaridae, with prey preference negatively correlating with shell weight (Dudgeon and Cheung Pui Shan, 1990). Cambarid crayfish have also been shown to be successful predators on gastropods (Crowl and Schnell, 1990; Alexander and Covich, 1991) and are capable of consuming >100 snails/day (Lodge et al., 1987).

The freshwater prawn *Macrobrachium lar* is abundant in Guam's streams and successfully preys on thiarid gastropods in the laboratory (F. Camacho, personal observation). While the shrimp and snail species co-occur in Guam's streams, the shrimp distributions appear to be influenced by physical barriers, such as waterfalls, where their predators are excluded (Parham, 1995). Generally, higher densities of snails occur in the presence of predators of *Macrobrachium* (e.g., the jungle perch

Kuhlia rupestris) while lower snail densities are usually in areas of high *Macrobrachium* abundance (F. Camacho, unpub. data). Thus, biotic interactions may be an important determinant of the abundances and distributions of freshwater gastropods in tropical streams of the Pacific.

Shell morphology has been implicated as an important feature in deterring marine predators (Vermeij, 1978) and may be an important determinant of gastropod vulnerability to predation by *Macrobrachium*. Important characteristics of marine snails are the presence of strong shell sculpture, low spires, and toothed apertures (Vermeij, 1978; Vermeij and Covich, 1978). However, these conspicuous elements are generally lacking in freshwater gastropods. Freshwater prawns peel gastropod prey with their mouth parts in a manner similar to that of panulirid lobsters, rather than crushing their shell with their chelae, as xanthid crabs and crayfishes do. Previous laboratory experiments have shown that *M. lar* has difficulty handling the thick-shelled, disc-shaped freshwater nerite *Neritina pulligera* (F. Camacho, pers. obs.), suggesting that sculpturing and shell width may be important in determining gastropod vulnerability to predation by *Macrobrachium*.

For this study, I describe the feeding behavior of *Macrobrachium lar* on the freshwater snail *Thiara granifera*. I then explore the relationship between aperture size of *Thiara granifera* and predator size of *M. lar*. Finally, I determine how shell width of *T. granifera* is related to shell lip strength and the degree of predator interest.

MATERIALS AND METHODS

Study Organisms

Thiara granifera (Prosobranchia: Thiaridae) is a parthenogenetic gastropod found in freshwater streams throughout Southeast Asia and the Indo-Pacific, and large populations inhabit the lower reaches of streams throughout southern Guam. Additionally, the snail occupies several lentic freshwater systems on Guam, including the Fena Lake reservoir. The species is generally characterized by rows of small tubercles ornamenting the entire shell (Abbott, 1952). On Guam, the periostracal covering of the shell ranges from yellowish to dark brown and may have small red-brown spots, particularly among juvenile snails (Abbott, 1952).

The amphidromous prawn *Macrobrachium lar* is distributed throughout Oceania. On Guam, the shrimp is found in inland freshwater ecosystems that are connected with the ocean. The prawn occurs in rivers and streams throughout the southern region of the island, as well as in freshwater streams of caves in the northern section of Guam. Members of the genus *Macrobrachium* are typically omnivorous and feed on detritus, filamentous algae, fish, and invertebrates, including gastropods (George, 1969).

Field Collections

Specimens of *Thiara granifera* were collected by hand from runs and pools in the Ugum River, Guam. In the Ugum River, *T. granifera* was abundant in certain sections of the lower reach but absent in the upper reaches. Snails were brought to the University of Guam Marine Laboratory and held in 12-l aquaria at ambient temperature (25°C ± 3°C).

Specimens of *Macrobrachium lar* were collected in shrimp traps and hoop nets from the upper reaches of the Asmafines River, a stream in southern Guam that has low gastropod densities at elevations above 25 m. *Macrobrachium lar* were separated into two size-classes based on carapace length (± 5.0 mm): "Small" prawns (i.e., 20.0 - 30.0 mm CL) and "Large" prawns (i.e., 30.0 - 40.0 mm CL). Each size class of *Macrobrachium* was held in separate 12-l aquaria and fed a daily diet of freeze-dried filamentous algae, ground commercially available catfish food, and brine shrimp (*Artemia*) flakes up until 24 hr prior to running the feeding experiments.

Because of the high frequency of eroded apices among local populations of *Thiara*, maximum shell length was considered to be a poor determinant of shell size. The body whorls of the snails, however, lacked extensive erosion. Therefore, maximum aperture width, or "MAW", (i.e., the section of the shell measured from the outer lip of the aperture to the widest section of the body whorl) was used to divide *T. granifera* into two size-classes of 1.0 - 6.0 mm MAW and 6.0 - 11.0 mm MAW.

Feeding Behavior

The feeding behavior of individual specimens of *M. lar* was observed in 12-l glass aquaria. Shrimp were presented with either single or multiple prey items of various sizes and the feeding habits (e.g., point of shell breakage, orientation of prey during attack, prey manipulation) were recorded.

Feeding Assays

Two feeding assays were conducted to compare predation success and attack frequency between two size classes of shrimp (CL 20 - 30 mm and CL 30 - 40 mm) and snails (MAW 1 - 6 mm and MAW 6 - 11 mm). For each feeding assay, nine large and nine small shrimp were individually held in 12-l glass aquaria and tested simultaneously. For the large shrimp, specimens in the upper range (>35 mm CL) of the size class were used whenever possible. Individual shrimp received 5 specimens of each of the two size classes of *Thiara,* and the shrimp was allowed to prey on the snails for approximately 18 hours. At the end of that period, the number of snails killed and attacked was recorded. Attacked snails included specimens that had been wholly or partially consumed and those that were living but had a damaged shell.

Estimation of Predator Interest

The relationship between release time and prey size was determined for *Macrobrachium lar* preying on *Thiara granifera.* Release time, an estimate of predator interest, was estimated by providing a snail of known aperture width to an individual shrimp and recording the number of minutes the shrimp attempted to prey upon the snail. Shrimp were timed from the moment contact was made with the prey item until the moment the prey was first released and the shrimp moved away from the snail. Only uneaten snails were considered for analysis.

Estimation of Shell Lip Strength

A penetrometer was used to determine the strength of the outer lip of the aperture of *Thiara granifera*. The device, similar to one used by Perron (1981), consisted of a pin held in place by a plexiglass plate upon which weights were added.

Prior to determining the lip strength, the maximum aperture width of each specimen of *Thiara granifera* was measured with a vernier caliper. Shells were then placed under the penetrometer and oriented such that the pin was impinging upon the inner surface of the shell at the edge of the lip most distal to the columella. Shell lip strength was determined by applying weights to the plexiglass plate in 20-g increments until the lip broke.

Statistical Analysis

Attack frequency was determined to be the number of *Thiara granifera* of a specific size class that was attacked (i.e., wholly or partially consumed, or living but with a damaged shell) per individual shrimp. With combined data for shrimp in both size groups, a paired t-test (BMDP New System, Inc., 1994) was used to determine if small and large prey were attacked at unequal frequencies. A 2 x 2 contingency table (1 degree of freedom) (Sokal and Rohlf, 1995) was constructed to test the independence of the attack frequencies between different predator and prey sizes (i.e., if attack frequency of large or small *Macrobrachium* was determined by prey size).

Predation frequency was considered to be the number of consumed snails of a specific size class per individual shrimp. As with attack frequency, a paired t-test was used to determined if small prey were consumed more frequently than large prey and to determine differences in predation frequency on snails by small and large predators. A 2 x 2 contingency table (1 degree of freedom) (Sokal and Rohlf, 1995) was constructed to test the independence of the frequency of predation between different predator and prey sizes (i.e., if predation frequency of large or small *Macrobrachium lar* was determined by prey size). Correlation coefficients were calculated for the relationship between shell maximum aperture width (MAW) and release time and for the relationship between MAW and shell lip strength.

RESULTS

Description of Feeding Behavior

Both size classes of *Macrobrachium lar* displayed similar behavior. *M. lar* typically initiated contact with its prey by seizing the snail with its first and sometimes third pereopods, bringing the shell to its mouth parts. Because the mouth parts come together in a ventral plane of symmetry, the shells are manipulated such that the spire of *Thiara granifera* is faced downwards or within a 90° radius to the right of the animal. *M. lar* rotated the shells such that the lip of the aperture was inserted into the mandibles, and the shrimp would usually begin peeling the shell immediately when possible. *M. lar* would continue to peel the shell in a counter-dextral direction, rotating the shell with its first and third pereopods until the body whorl was sufficiently exposed to consume the prey or until the shrimp gave up. It appeared that the greatest difficulty in peeling the shell came when either the lip of the aperture was too thick to break or when the shrimp began peeling at the dorsal portion of the body whorl and could no longer crush the shell efficiently between its mandibles.

Small specimens of *Thiara granifera* (MAW < 3 mm) were grasped by the first pereopods of *Macrobrachium lar* and brought to the mandibles. The prawn either peeled the lip of the aperture or began crushing the shell from the apex of the spire anteriorly towards the body whorl. The smallest prey were almost completely consumed, leaving few shell fragments to determine how the shell was broken. However, small snails were occasionally found alive with only the body whorl remaining.

Attack Frequencies

Shrimp attacked both size classes of snails at high frequencies, inflicting sublethal to lethal damage upon most of the snails. The combined attack frequencies of large and small shrimp on either small or large snails revealed that small snails were attacked at significantly higher frequencies ($t = -3.7638$; $p = 0.0006$; Table 1). The mean attack frequency by large shrimp was 4.3 snails attacked/shrimp, while small shrimp had a mean attack frequency of 3.5 snails attacked/shrimp (Figure 1). In only two cases were the numbers of large snails attacked greater than the number of small snails attacked. Large and small shrimp attacked snails with about the same frequencies (Table 1), and there was no significant interaction between predator size and snail size on frequency of attack ($\chi^2 = 0.0071$; $p = 0.9331$; Table 1).

Predation Frequencies

Both the large and small size classes of shrimp were more successful at preying on small snails than on large snails ($t = -8.1287$; $p = 6.41 \times 10^{-9}$; Table 2; Figure 2). The relative numbers of each size of snail eaten were independent of predator size ($\chi^2 = 1.1606$; $p = 0.2813$; Table 2). Predation on the smaller snails by

Table 1. A 2 x 2 contingency table of the frequency of attack on the snail *Thiara granifera* by the prawn *Macrobrachium lar*. *Thiara granifera* were represented by two size classes: "Small" (1 - 6 mm MAW) and "Large" (6 - 11 mm MAW). *Macrobrachium lar* was separated into "Small" (25 - 30 mm CL) and "Large" (30 - 35 mm CL) size classes. Attacked specimens included consumed snails as well as snails whose shell was damaged as evidenced by chipped or crushed surfaces after presentation to a shrimp.

	Snail Size (a = 2)			
Shrimp Size (b = 2)	Large snails	Small snails	Totals	% Large snails/ Total snails attacked
Large shrimp	71	83	154	46.1
Small shrimp	57	68	125	45.6
Totals	128	151	279 = *n*	91.7

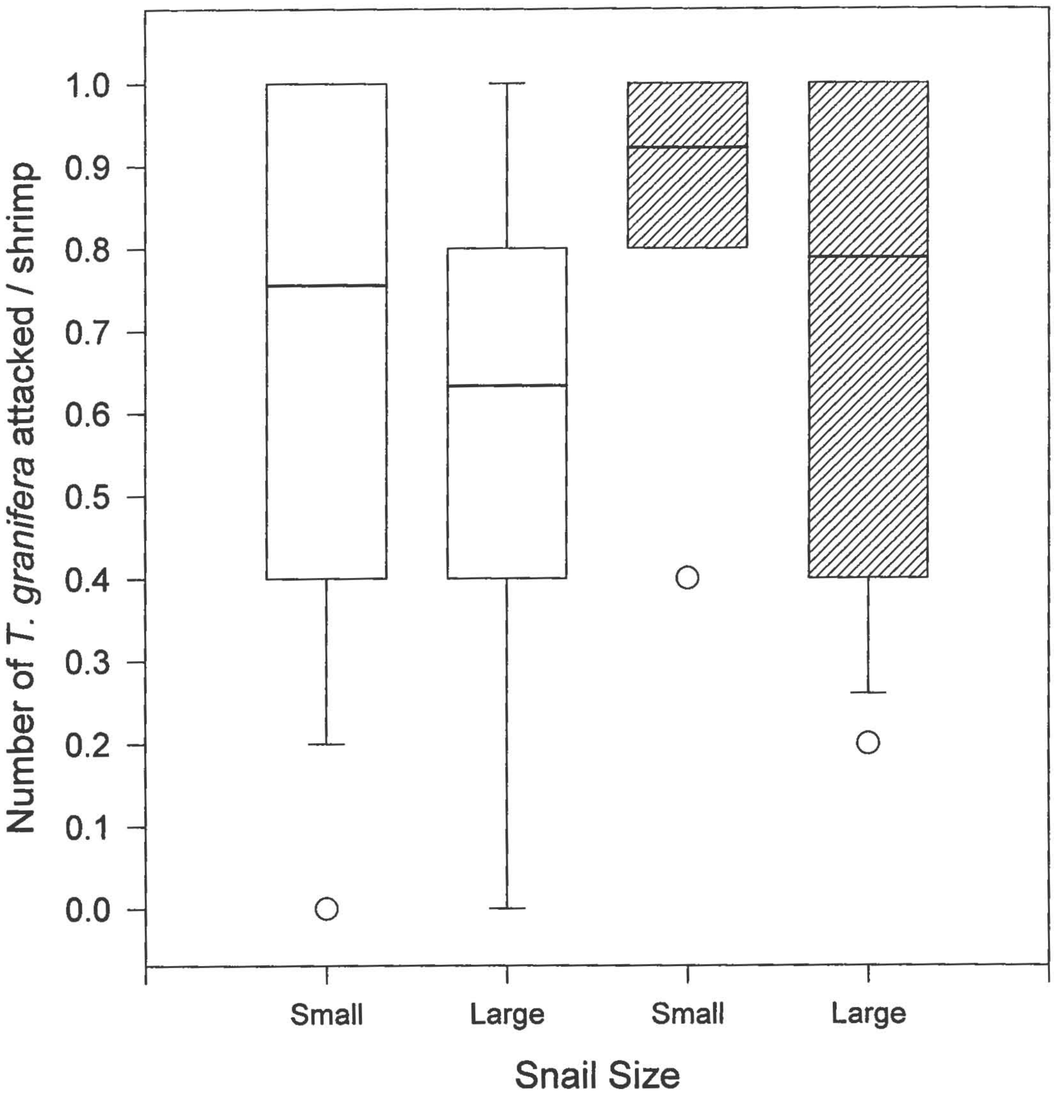

Figure 1. Boxplot of attack frequency of "Small" (CL 20-30 mm; open boxes) and "Large" (CL 30-35 mm; hatched boxes) specimens of *Macrobrachium lar* on "Small" (MAW 1-6 mm) and "Large" (MAW 6-7 mm) specimens of *Thiara granifera*. Attacked snails were those which were wholly or partially consumed or were living with a broken shell. Heavy horizontal lines represent the mean attack rate. Capped vertical bars signify 25th and 75th percentiles, open circles represent the extent of data outside the 10th and 90th percentiles.

Table 2. A 2 x 2 contingency table of the frequency of predation on the snail *Thiara granifera* by the prawn *Macrobrachium lar*. *Thiara granifera* were represented by two size classes: “Small” (1 - 6 mm MAW) and “Big” (6 - 11 mm MAW). *Macrobrachium lar* was separated into “Small” (25 - 30 mm CL) and “Large” (30 - 35 mm CL) size classes.

	Snail Size (a = 2)			
Shrimp Size (b = 2)	Big snails	Small snails	Totals	% Large snails/ Total snails consumed
Big shrimp	6	45	51	11.8
Small shrimp	3	49	52	5.8
Totals	9	94	103 = *n*	17.5

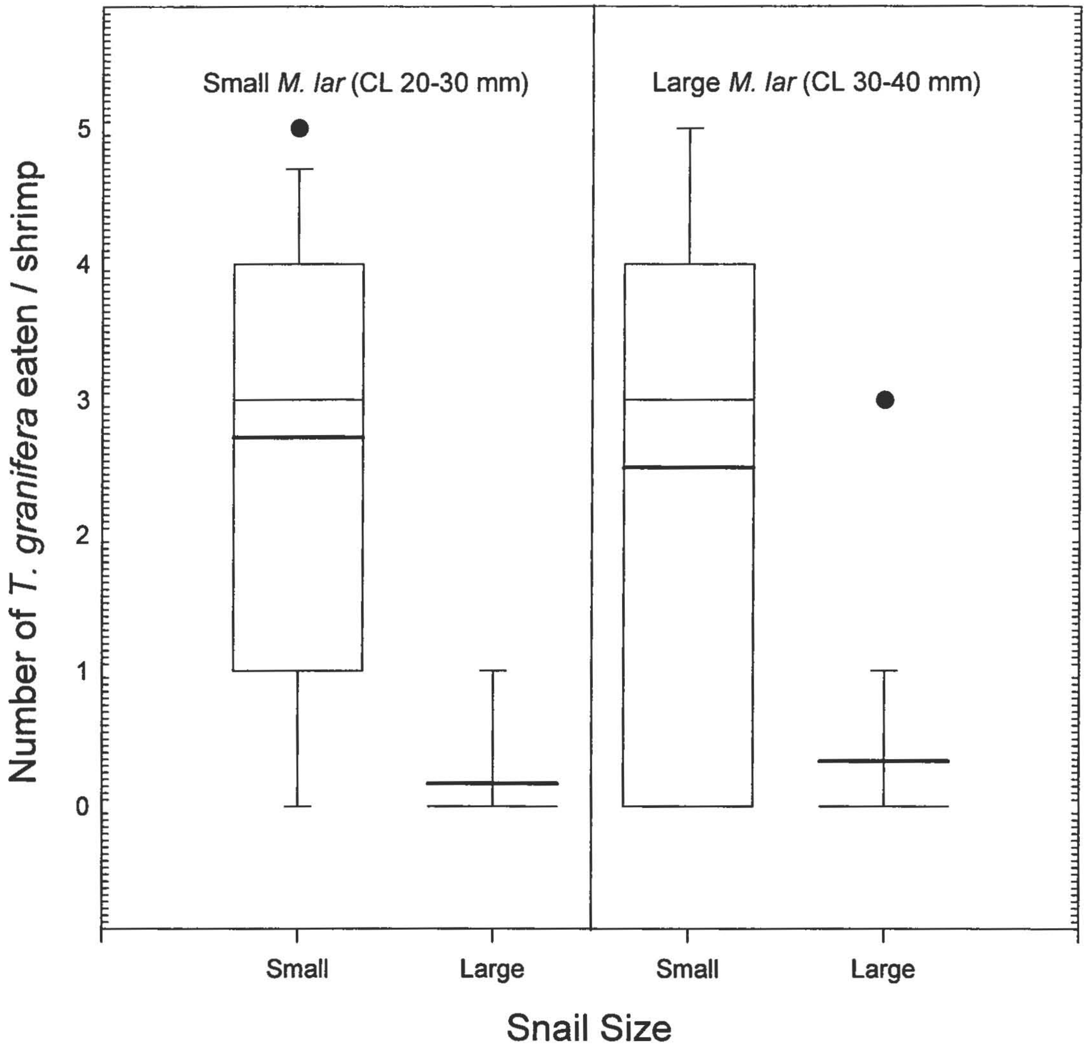

Figure 2. Boxplot of predation frequency of "Small" (CL 20-30 mm) and "Large" (CL 30-35 mm) specimens of *Macrobrachium lar* on "Small" (MAW 1-6 mm) and "Large" (MAW 6-11 mm) specimens of *Thiara granifera*. Heavy horizontal lines represent the mean predation frequency. Capped bars signify 25th and 75th percentiles; open circles represent the extent of data outside the 10th and 90th percentiles.

individual shrimp ranged from 0 snails consumed to total consumption of the small snails for both the small and large shrimp. In only one case was the number of large snails consumed greater than the number of small snails eaten.

Predator Interest and Shell Lip Strength of *T. granifera*

There was a significant positive correlation between lip strength and maximum aperture width of the shells of *Thiara granifera* ($r = 0.67$; $p = 0.0026$; Figure 3). Over 40% of the variation between shell lip strength and shell width was attributed to the correlation between the two factors.

To achieve better linearity of the relationship between release time and shell MAW, release times were log-transformed and plotted against aperture width (Figure 4). The degree of predator interest of big *Macrobrachium lar* in *Thiara granifera* declined significantly as the aperture width of the shell increased ($r = 0.6301$; $p = 0.0157$; Figure 4), indicating that more than 30% of the variation in release time is due to variation in shell width or some factor associated with shell width.

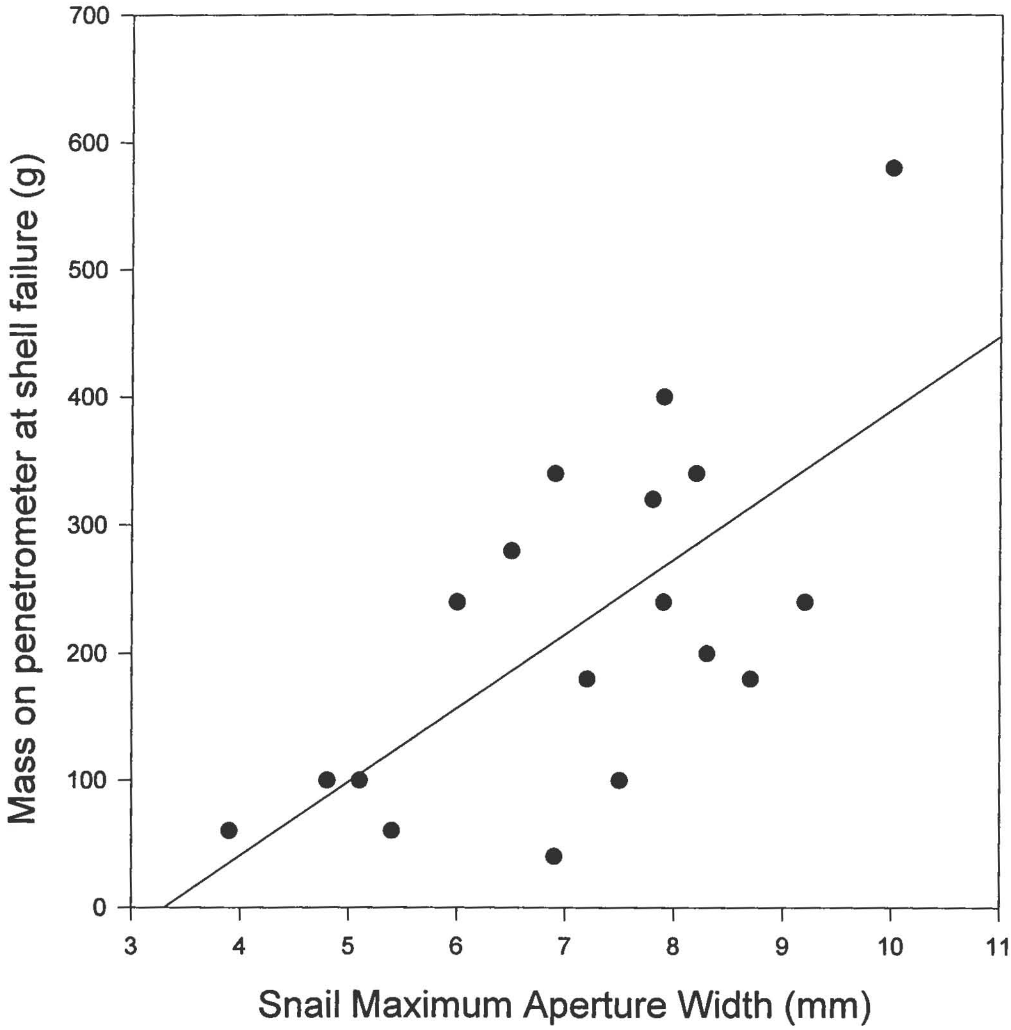

Figure 3. Plot of shell lip strength (i.e., mass on the penetrometer at the moment of shell failure) of *Thiara granifera* on shell maximum aperture width.

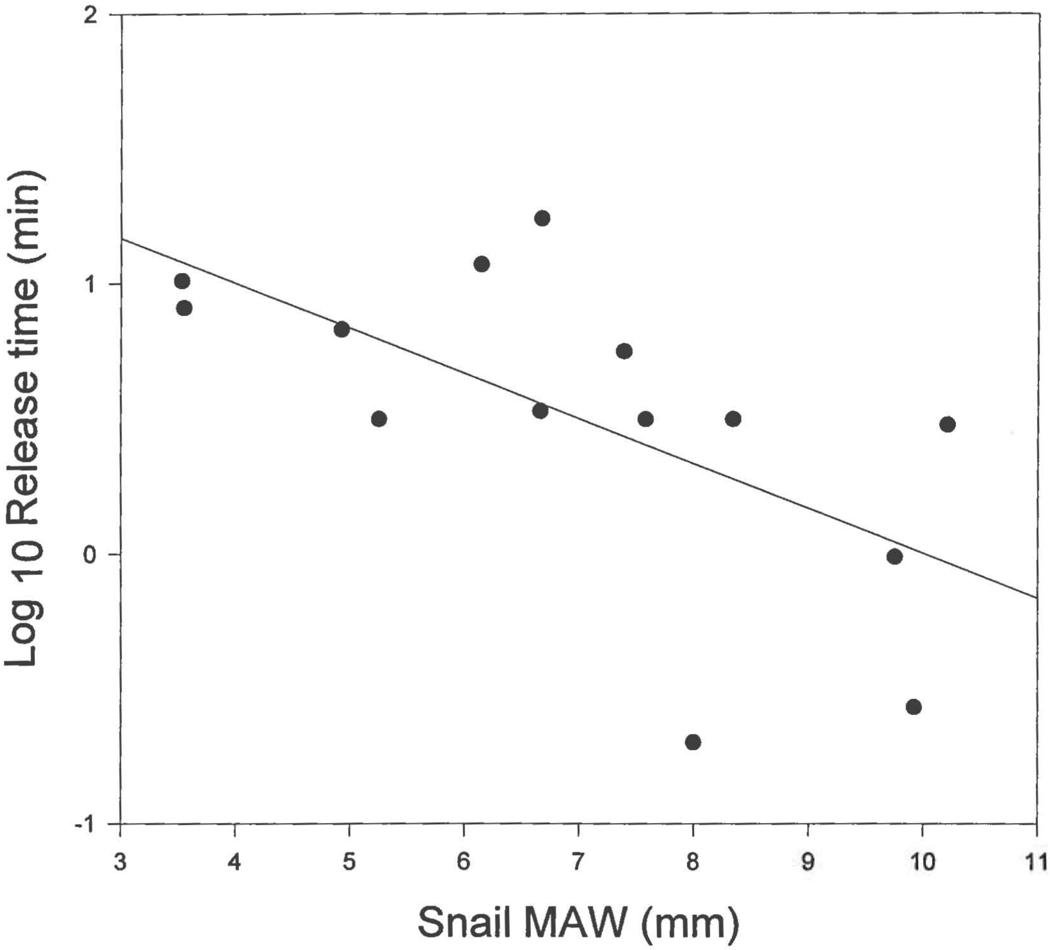

Figure 4. Plot of $\log_{10}$ release time of *Macrobrachium lar* on shell maximum aperture width. Release time (an estimate of predator interest) was estimated as the amount of time *M. lar* handled a specimen of *Thiara granifera* of known aperture size. Timing was recorded from the moment a shrimp first made contact with the snail until the shrimp released and abandoned the prey. Only unconsumed, attacked snails were analyzed.

DISCUSSION

Certain aspects of the feeding behavior of *Macrobrachium lar* resemble that of spiny lobsters (Palinuridae) (Herrnkind et al., 1975) and the freshwater crab *Somaniathelphusa sinensis* (Dudgeon and Cheung Pui Shan, 1990). For example, *Panulirus argus* and *S. sinensis* hold their prey with their first and third chelipeds and initiate peeling on the outer lip of the aperture (Herrnkind et al., 1975) in the same manner as *M. lar*. Generally, the use of mouth parts to peel shells is uncommon among decapod crustaceans, with the majority using well-developed chelae for crushing shells. The chelae of *M. lar* are poorly suited for crushing shells as they lack the musculature and skeletal thickness found in chelae of marine crabs such as *Etisus* and *Carpilius*. Additionally, the lack of involvement of the second chelae of *M. lar* in peeling *T. granifera* is not surprising because the chelae lack specialized structures for peeling that are common among members of the marine crab genus *Calappa*. Generally, the second chelae of the prawn are used for agonistic behavior towards conspecifics (Donaldson, 1981).

Smaller specimens of *Thiara granifera* are more vulnerable to predation by shrimp of all sizes. This results from the higher probability of predation by large and small shrimp on small snails. Aperture width, or a factor that increases allometrically with aperture width (e.g., shell thickness, mass of the prey, shell length), affects predation success of *Macrobrachium lar*. The higher attack frequencies on small snails by all sizes of shrimp and increased predator interest (i.e., release time) in small shrimp suggest that the shrimp possess a certain degree of preference for smaller snails than larger ones. This is probably a result of physical inability of many of the shrimp to consume the larger snails. It is likely that *Thiara granifera* attain a refuge in size from predation by most sizes of *Macrobrachium lar*. The high variability in the attack and predation frequencies also suggests that some individuals are more adept at preying on snails than others.

The results of the feeding assay are consistent with similar studies of freshwater crustaceans. The freshwater crab *Somaniathelphusa sinensis* demonstrates a significant preference for small specimens of the pulmonate snail *Biomphalaria straminea* (Dudgeon and Cheung Pui Shan, 1990). Similarly, small specimens of *Macrobrachium rosenbergii* have difficulty consuming large individuals of the snail *Biomphalaria glabrata* but readily eat small specimens of the snail (Roberts and Kuris, 1990).

The presence of high spires and the ability to retract deep into the body whorl aid cerithid and terebrid snails in thwarting peeling predators in marine environments (Vermeij, 1978). *Thiara granifera* also possesses these antipredatory features, which appear to hinder *Macrobrachium lar* from successfully consuming large *Thiara granifera* and probably account for the generally lower success of peeling predators on freshwater thiarids when compared to pulmonate snails. Typically, prosobranch snails possess thicker shells and opercula, while pulmonate snails are generally thin-shelled and lack opercula (Vermeij and Covich, 1978). The crab *Somaniathelphusa sinensis* preferrentially consumed pulmonate snails over the thiarid gastropod *Melanoides tuberculata* because of the lower energy return (i.e., tissue dry mass/handling time) for *M. tuberculata* (Dudgeon and Cheung Pui Shan, 1990). Preliminary observations of *M. lar* preying upon lymnaeid snails show that the prawn preys more successfully on thin-shelled *Lymnaea* sp. than on specimens of *Thiara granifera* of similar aperture width (F. Camacho, pers. obs.).

The effects of biotic interactions in determining abundances and distributions of freshwater organisms are poorly known for tropical Pacific insular stream ecosystems. Predation has been implicated as a strong selective force in tropical marine systems (Vermeij, 1978), but its importance in freshwater habitats has only recently been explored. This study is the first report of *Macrobrachium lar* predation on freshwater gastropods and suggests that the prawn could influence the distribution of *Thiara granifera* in natural habitats.

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